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THE VALIDITY AND RELATIONSHIPS OF *PRINIA GRACILIS NATRONENSIS* (AVES: SYLVIIDAE)

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Abstract.—Analysis of six morphological and plumage coloration characters of *Prinia gracilis* from the Nile Delta, Wadi Natroun, lower Nile Valley, and Faiyum shows that *P. g. natronensis* Nicoll of Wadi Natroun is a distinct subspecies. *Prinia g. natronensis* is more closely related to *P. g. deltae* Reichenow of the Nile Delta west of 32°E than to *P. g. gracilis* (Lichtenstein) of the Nile Valley and Faiyum. Evidence for the sequence of geological and climatic events that led to the isolation of Wadi Natroun from the Nile Delta and Valley supports this conclusion.

Five subspecies of the Graceful Warbler, *Prinia gracilis,* are currently recognized as occurring in Egypt (Meinertzhagen 1930; Vaurie 1959). One of these, *P. g. natronensis* Nicoll is confined to Wadi Natroun, a small depression in the northeastern portion of the Egyptian Western Desert. Two others important for this review are *P. g. gracilis* (Lichtenstein) of the Nile Valley south at least to Khartoum and the Faiyum, and *P. g. deltae* Reichenow from the Nile Delta. Vaurie (1959) considered *P. g. deltae* polytopic, and reoccurred up the Nile Valley at Luxor. Specimens from the Nile Delta east of 32°E to the Suez Canal were not included in the present analysis because that area appears to be a zone of intergradation between *P. g. deltae* and *P. g. palaestinae* (Zedlitz) of the Sinai and southern Israel. In Nicoll's (1917) description of *P. g. natronensis,* he characterized it as similar to nominate *P. gracilis,* but with a longer bill. In his monumental review of Palearctic passerines, Vaurie (1959) described *P. g. natronensis* as having "somewhat longer" bills and more sharply and darkly streaked upperparts than nominate *P. gracilis.* However, Vaurie measured but six adult specimens from Wadi Natroun and concluded that *P. g. natronensis* was only a "moderately well-differentiated subspecies" (1959:306). I have been able to examine 23 specimens from Wadi Natroun, including the holotype, and can offer some remarks on the systematic status of *P. g. natronensis* and its relationship to nominate *P. gracilis* and *P. g. deltae.* More material and field work is needed to evaluate the subspecific relationships of the populations inhabiting the Nile Delta east of 32°E, the Sinai, southern Israel and the Nile Valley south of the Faiyum area.

Materials and Methods

The following six measurements were taken (all in mm): Exposed culmen.—Measured from base of feathering on the forehead to maxilla tip. Bill from anterior edge of nostril.—Measured from anterior edge of nostril to maxilla tip. Gonys.—Measured from junction of rami to mandible tip. Wing.—Measured from bend of flattened wing at carpal joint to longest primary tip. Tail.—Measured from insertion of longest rectrices (always middle pair) to distal tip. Tarsus.—Measured

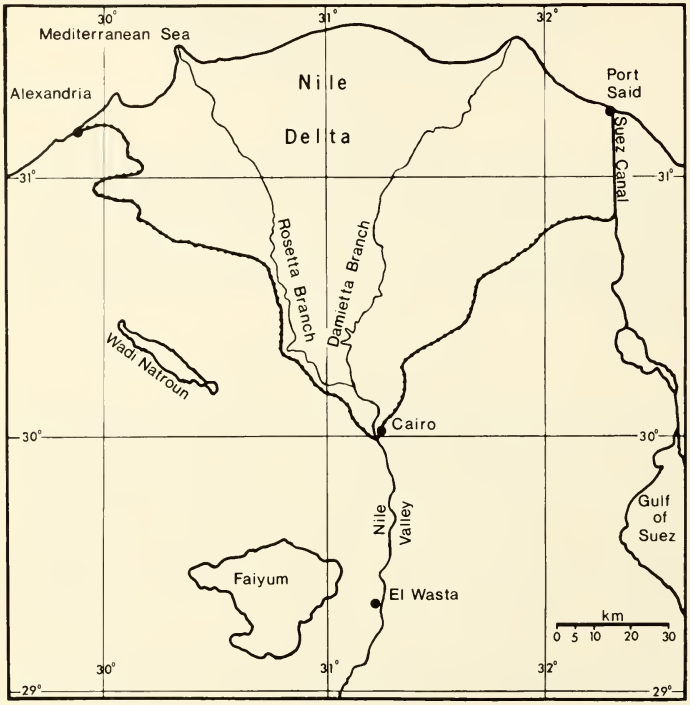

Fig. 1. Map of Egypt north of the Faiyum, including Wadi Natroun.

from junction of tibiotarsal-tarsometatarsal joint to distal edge of distalmost undivided scute overlying toes (little variation was found in the scutellation pattern of the feet). In cases when the sex designation on the specimen tag was lacking, ambiguous, or suspected of being inaccurate the specimen was classified as unsexed. Vernier calipers were used to measure the bill and tarsus to the nearest 0.1 mm, and a rule for the wing and tail to the nearest 1.0 mm.

Graceful Warbler specimens were examined from 33 localities in the Nile Delta and Valley, the Faiyum and Wadi Natroun (Appendix 1). Since adequate samples were not available from several localities, specimens were pooled into four Operational Taxonomic Units (OTUs) representing broader geographical areas (Fig. 1). These include: 1) Cairo—the environs of Cairo including Abu Rawash, south along the Nile Valley to El Wasta; 2) Wadi Natroun; 3) Nile Delta—areas of the Nile Delta west of 32°E; 4) Faiyum.

Statistical tests used MIDAS programs, written by the University of Michigan Statistical Research Laboratory. Differences among means and variances were tested by Student's *t*-test or analysis of variance (ANOVA), as appropriate. When the ANOVA showed significant variation, a Scheffé test was used to determine which means were significantly different. The Scheffé tests were also used in pairwise combinations to test differences between OTUs. Principal component analyses used a correlation matrix between unstandardized characters. Probabilities of 0.05 or less are considered statistically significant and sufficient to reject the null hypothesis.

Description of Wadi Natroun

Wadi Natroun is a narrow depression, approximately 250 km^2 in area, located southwest of the Nile Delta, from 30°17′ to 30°38′N and 30°2′ to 30°30′E. The depression is completely separated from the Nile Delta by barren desert, and its eastern edge is approximately 40 km from the Nile Delta. The lowest point is at Umm Risha, 21.9 m below sea-level.

Towards the center of the depression are a series of salt-water lakes aligned parallel to its main axis. The dominant vegetation along the edges of these lakes is *Cyperus* (cf. *laevigatus*), *Typha, Scirpus,* and *Phragmites.* The ground tends to be very muddy and encrusted with salts, principally Na_2CO_3 and $NaHCO_3$ (Abdel Salim 1966). It is interesting to note that the only known stand of wild Papyrus (*Cyperus papyrus*) in Egypt is along the edge of Lake Umm Risha (El Hadidi 1971).

Wadi Natroun has a very arid climate. The following meteorological data were compiled from Abdel Salim (1966). Between 1946–1955 the annual mean temperature was 22.8°C with the absolute extremes of 46.7°C in July (mean range 36.4°C–20.6°C) and 1.0°C in January (mean range 20.6°C–7.2°C). Depending on the season the prevailing winds come from just about every compass direction, and range in mean velocity from 10.9 km/hr in December to 19.8 km/hr in June. The average rainfall is 55.1 mm with 80% falling in November and December.

In the Pliocene Wadi Natroun was the western swampy edge of the Paleonile (Said 1975). It has been proposed that the post-Pliocene extreme western edge of the Nile extended from Abu Rawash (northwest of Cairo) to the eastern end of Wadi Natroun (Sandford and Arkell 1939). If this was the case, then at least up until the early Pleistocene Wadi Natroun and the former Nile Delta would have been connected by a vegetated zone.

The upper geological strata of the area between Wadi Natroun and the western edge of the modern Nile Delta can be divided into two distinct groups. Along the northeastern edge of the depression is a terraced slope that rises to +35 m and gently slopes towards the central lakes (Shata and El Fayoumy 1967). Running along the eastern edge of this marginal slope in a NW-SE direction and transversing the area to the western edge of the Nile Delta is a gravel ridge of the Tahreer or El Tahrir soil type (Abdel Samie 1967; Shata and El Fayoumy 1967). This ridge is endogenous in nature and is composed of nilotic gravels laid down in the early Pleistocene (Shata and El Fayoumy 1967). In the early Pleistocene a series of declines in the water table resulted in the gradual retreat of an ancient Wadi Natroun lake and the terracing of the marginal slope. This lake dried up in the late Sebilian (post-Middle Paleolithic, Sandford and Arkell 1939), by which time

Wadi Natroun was completely separated from the Nile Delta (Shata and El Fayoumy 1967). During the Holocene the water table rose, flooding some of the lower areas of the former Wadi Natroun Lake (Shata and El Fayoumy 1967), but never resulting in a "green-connection" between Wadi Natroun and the Nile Delta.

Brief Notes on the Habitat and Natural History of *P. gracilis*

Prinia gracilis is a characteristic bird of the vegetated portions of the Nile Delta and Lower Valley. This species is common and conspicuous in low vegetation, particularly matted-grass and reed-clumps. In Wadi Natroun the Graceful Warbler is a common nesting bird in the reed-beds along the marshy margins of the lakes. Loat (1905) described them as "not uncommon" in Wadi Natroun "amongst the *bourdy*" (generic for *Typha* and *Cyperus,* fide Täckholm, 1974).

At Wadi Natroun in early May 1981 Mr. Sherif Tewfik and I found pairs of *Prinia gracilis* in various stages of breeding, from nest construction to feeding young. Singing males were more common along the lakes in the very marshy spots than in the somewhat drier upland areas. Cows, donkeys, and a few goats roamed free around the lakes and grazed on the vegetation, but because they tended to limit their grazing to the drier areas, they probably interfere very little with *Prinia.*

Although no detailed study of marked individuals has been conducted, Simmons (1954) found that near Suez paired adults remain in the general vicinity of the breeding area throughout the year, while juveniles disperse from the natal territory soon after fledging. Graceful Warblers are primarily ground foragers and insectivorous (Simmons 1954; pers. obs.).

There is good evidence that Graceful Warblers do not disperse over expanses of barren desert. Although similar habitats exist in the oases of the Egyptian Western Desert, as in portions of the Nile Valley and Delta, Graceful Warblers have never been recorded in the former (Moreau 1934; Al-Hussaini 1959; pers. obs.). Thus, the desert acts as a physical barrier to dispersal and limits genetic exchange between disjunct populations. The dispersal of juvenile Graceful Warblers recorded by Simmons (1954) in the Nile Delta was probably local.

This species is sexually monomorphic (Meinertzhagen 1954), and the recorded variation in bill color is seasonal and age related (Ali and Ripley 1973; pers. obs.) rather than sexual (cf. Simmons 1954). In all of the Egyptian populations that I have looked at, breeding adult males and females have black bills. Meinertzhagen (1930) described immatures as duller than adults; while Ali and Ripley (1973) characterized immatures as more shadowy and broadly streaked on the upperparts and with a distinct yellow tinge to the sides of the neck and upper breast. These characters are difficult to discern and I know of no plumage color characters that allow reliable separation of immatures and adults. Further, I was unable to separate immatures from adults using feather wear or molt sequence. In almost all cases nothing was noted on the specimen labels about skull ossification, and consequently immatures could not be readily distinguished from adults.

Results

Of the 23 specimens examined from Wadi Natroun, two were not measured and 10 were unsexed. Descriptive statistics of male, female and unsexed Graceful

Table 1.—Measurements (mm) of *Prinia gracilis natronensis* collected in Wadi Natroun.

	Female	Male	Unsexed
Culmen			
n	5	6	10
Range	9.6–10.9	9.7–11.3	10.0–11.1
Mean	10.26	10.36	10.60
SD	0.49	0.66	0.33
Bill from ant. edge nostril			
n	5	6	10
Range	6.3–7.3	6.2–7.7	6.5–7.3
Mean	6.84	7.00	7.04
SD	0.42	0.50	0.21
Gonys			
n	4	4	10
Range	5.7–6.9	5.2–7.2	6.2–7.3
Mean	6.30	6.57	6.69
SD	0.51	0.92	0.35
Wing			
n	4	6	10
Range	42–46	42–47	42–44
Mean	44.25	45.33	42.90
SD	1.70	1.75	0.87
Tail			
n	3	6	2
Range	50–66	55–64	53–60
Mean	57.6	60.5	56.5
SD	8.02	3.39	4.94
Tarsus			
n	5	6	8
Range	18.3–19.2	18.5–19.7	17.3–18.9
Mean	18.76	19.06	17.90
SD	0.36	0.47	0.52

Warblers from Wadi Natroun are summarized in Table 1. A series of *t*-tests comparing males and females for each of the six characters revealed no significant sexual dimorphism. No significant differences were found between the unsexed birds and males and/or females. A similar series of tests was run for the sex classes of specimens from the other three OTUs. In no case was a significant difference found in intra-OTU variation of single characters, so the three sex classes (males, females and unsexed) were combined in further tests.

Since immature and adult Graceful Warblers could not be separated by plumage differences, it was not possible to take ontogenetic variation directly into account. However, if significant ontogenetic differences exist for any character within an OTU and different age classes are represented in the sample, then such characters should have a multi-modal distribution. Only uni-modal distributions for each character were found, and it is assumed that immatures cannot be separated from

Table 2.—Measurements (mm) of *Prinia gracilis* from four areas in Lower Egypt.

	Cairo to El Wasta	Wadi Natroun	Nile Delta W of 32 E	Faiyum
Culmen				
n	25	21	8	6
Range	8.1–11.2	9.6–11.3	10.1–11.5	9.1–9.7
Mean	10.06	10.45	10.45	9.40
SD	0.68	0.48	0.43	0.25
Bill from ant. edge nostril				
n	25	21	8	7
Range	5.2–7.1	6.2–7.7	6.3–7.2	6.0–6.5
Mean	6.46	6.98	6.70	6.31
SD	0.42	0.35	0.26	0.22
Gonys				
n	25	18	8	7
Range	5.8–7.0	5.2–7.3	6.1–7.0	5.5–6.7
Mean	6.45	6.57	6.53	6.17
SD	0.38	0.53	0.36	0.47
Wing				
n	25	20	8	7
Range	41–46	42–47	42–49	41–46
Mean	43.36	43.90	44.75	43.71
SD	1.41	1.68	2.43	1.88
Tail				
n	24	11	7	7
Range	44–66	50–66	53–67	48–63
Mean	57.41	59.00	60.71	56.42
SD	5.61	4.91	4.78	5.79
Tarsus				
n	24	19	8	7
Range	16.5–19.3	17.3–19.7	17.4–18.9	16.8–18.4
Mean	18.02	18.49	18.46	17.81
SD	0.66	0.69	0.50	0.58

adults by size. Descriptive statistics of the six characters for the four OTUs with sex classes combined are presented in Table 2.

Of the six characters measured only the culmen, bill from anterior edge of nostril and tarsus showed significant inter-OTU variation ($F = 6.54$, $P = 0.007$; $F = 9.95$, $P = 0.00001$; $F = 3.12$, $P = 0.03$, respectively). When all six characters were individually compared in pairwise combinations between OTUs several distinct patterns were found (Table 3).

The mean culmen length of Wadi Natroun birds was significantly different from the Cairo and Faiyum OTUs, whereas this was not the case between the Delta and Wadi Natroun OTUs. Further, the Faiyum birds were significantly different from those of the Delta and Cairo OTUs. The mean length of the bill from the anterior edge of the nostril showed a similar pattern, in that birds from Wadi Natroun were highly significantly different from the Faiyum and Cairo OTUs.

Table 3.—Matrices of *F*-statistics by OTUs for each character[1]

	Culmen/bill from ant. edge of nostril				Gonys/wing				Tail/tarsus			
OTU	1	2	3	4	1	2	3	4	1	2	3	4
1		22.94***	0.92	2.53		1.10	0.23	3.98		5.52*	0.56	2.71
2	5.42*		17.55***	3.43	0.76		0.06	1.40	0.65		5.58*	0.01
3	6.94*	16.62***		4.17*	2.19	4.12*		1.36	0.18	0.97		3.70
4	2.84	0.00	12.16**		0.14	0.04	2.09		2.02	0.43	2.21	

[1] Character to the left of slash is on bottom half of matrix, character to the right of slash is on the top half of matrix. See Materials and Methods for identification of numerical OTUs. One asterisk $P < 0.05$, two asterisks $P < 0.01$, three asterisks $P < 0.001$.

Also, the Faiyum and Delta OTUs showed a significant difference. The only significant interlocality difference in the mean gonys measurement was between the Wadi Natroun and the Faiyum OTUs. For the wing no distinct differences were found between OTUs, although the Delta and Cairo OTUs were border line ($F = 3.98$, $P = 0.051$). The variance of the tail length was relatively large (Table 2), and this character revealed no significant differences or information on relationships between the OTUs. The mean tarsus length showed a similar pattern as the first two characters; birds from Wadi Natroun were significantly different from the Faiyum and the Cairo OTUs.

The results of the inter-OTU Scheffé pairwise comparisons for the six characters can be summarized as follows:

1) The wing and tail revealed no significant patterns and can be excluded as characters yielding information on inter-OTU relationships.
2) The Wadi Natroun OTU was significantly different in 3 of the remaining 4 characters from the Cairo OTU, and in 4 of 4 characters from the Faiyum OTU.
3) No significant differences were found between the Wadi Natroun and Nile Delta OTUs.
4) The Faiyum and Cairo OTUs are more closely related to one another than either is to the other two OTUs.

For the Principal Components (PC) analysis only the four characters that showed inter-OTU differences were used (culmen, bill from anterior edge of nostril, gonys and tarsus). The loadings of these four characters for the first three PCs are presented in Table 4. PC I accounts for 46.3% of the phenetic variation. All loadings for PC I are positive and it is presumed to be primarily a size component. The highest loading for PC I is the bill from anterior edge of nostril. PC II explains an additional 25.2% of the phenetic variation. The highest positive loading for this component is the tarsus, while the culmen and gonys have negative loadings.

The four OTUs separate into two groups over the two-dimensional projection of the first two principal components (Fig. 2). The Wadi Natroun birds tend to cluster in the upper portion of the projection, with those from the Delta, but are somewhat separate. The Cairo OTU is widely distributed in the bottom half of the projection. The Faiyum OTU is spread throughout the Cairo OTU.

Table 4.—Character loadings and explained variances of the first three principal components.

Character	I	II	III
Culmen	0.45	−0.57	0.53
Bill from ant. edge of nostril	0.67	0.02	0.06
Gonys	0.48	−0.07	−0.79
Tarsus	0.33	0.82	0.30
% of total variance explained	46.3	25.2	20.7

Discussion

Historically in passerine systematics a combination of differences in plumage coloration and morphological measurements has been used to separate distinct populations into subspecies. It is important to distinguish between types of geographical variation and their use in interpreting infraspecific relationships. In many cases characters show smooth clinal variation within the contiguous range of a species, and arbitrary designations are drawn to separate portions of the cline into subspecies. This typological approach to subspecies has come under a considerable amount of criticism, for no real taxonomic information is presented by subspecific names used in this way (see Wilson and Brown 1953, for an early review of this misuse). However, for some characters which show clinal patterns, abrupt changes in morphology or plumage coloration occur between continuous populations; in this case they can be separated in a non-arbitrary way. These stepped clines may be the result of interspecific competition or some abrupt change in ecological parameters such as climate, soil types or vegetation cover. In other cases insular or geographically disjunct forms show distinct color or morphological differences which are not part of a broad clinal pattern. Such allopatric populations may experience different ecological restraints and have little genetic exchange with other populations. Both for stepped clines and distinct allopatric populations taxonomic information on infraspecific relationships and divergence between populations is useful to acknowledge and can be represented by a trinomial.

The results of the Scheffé and Principal Component analyses indicate that at least two distinct groups are present in the sample; birds from the Cairo and Faiyum OTUs, and birds from the Wadi Natroun and Delta OTUs. The ranges of measurements for these two groups overlap to such an extent they cannot solely be used to separate them. The only exception is the length of the bill from anterior edge of nostril, which shows only a small amount of overlap. Thus two morphologically distinct groups can be recognized in Egypt.

Size variation between the OTUs has a distinct pattern. For four of the six characters, the Wadi Natroun OTU is larger than or equal to the Delta OTU in mean character lengths, and for all six characters is larger than the Cairo and Faiyum OTUs. Excluding the Wadi Natroun OTU, the Delta OTU is always the largest, followed by the Cairo, then the Faiyum OTUs, except in one case (wing) when the Faiyum OTU is larger than the Cairo OTU.

No distinct plumage differences are apparent between Graceful Warblers from the Cairo and Faiyum OTUs. However, these birds are distinguishable from specimens collected in Wadi Natroun by having lighter brown and less sharply streaked upperparts. Specimens from the Delta OTU are generally discernable

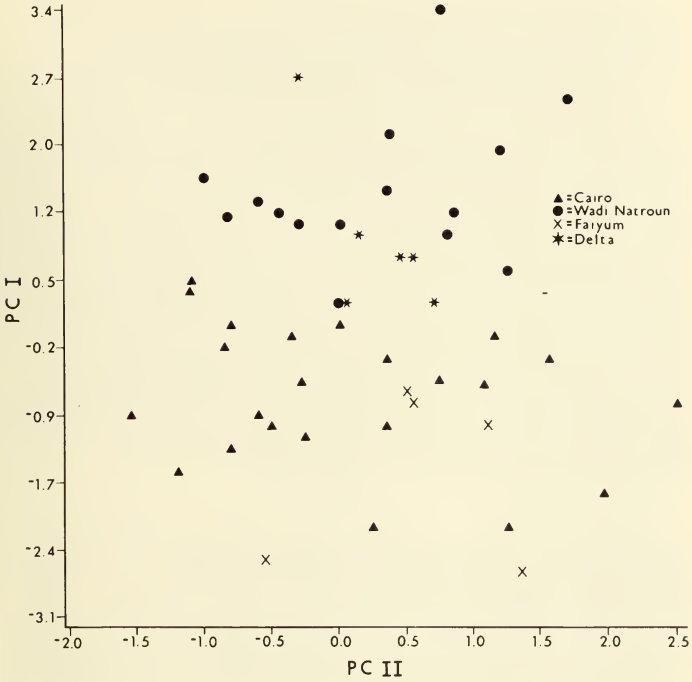

Fig. 2. Two-dimensional projection of the first two principal components (PC) for four morphological characters.

from Wadi Natroun birds by their darker and more broadly streaked upperparts. The trend in plumage coloration runs from the Delta where birds are the darkest, to Wadi Natroun, and then to the lower Nile Valley and Faiyum where birds are the lightest.

The patterns in measurements and plumage coloration differ between the OTUs. Based on the combination of the two types of characters the following subspecies are recognized:

P. g. deltae.—Occurring in the Nile Delta west of approximately 32°E. Morphologically similar to *P. g. natronensis* but separable by the distinctly darker and more saturated brown upperparts with broader streaks. Larger and slightly darker than *P. g. gracilis.*

P. g. natronensis.—Restricted to Wadi Natroun. Similar to *deltae* except as noted above. Separable from *P. g. gracilis* by having slightly darker and more

broadly streaked upperparts. It should be noted that the type of *natronensis* (BMNH 1917.1.12.2) is an exceptionally light individual and does not properly represent the typical coloration of this species from Wadi Natroun.

P. g. gracilis.—Occuring from the Cairo region south along the Nile Valley and in the Faiyum. Smaller and lighter than *deltae* and *natronensis* as noted above.

The geological history of the area indicates that continuous vegetation existed during the post-Pliocene between Wadi Natroun and the Nile Valley and Delta. Presumably if *Prinia gracilis* occurred in the region at this time, the populations were probably not differentiated because of genetic exchange across the vegetated zones. In the Pleistocene, as the area experienced desiccation (Butzer 1975), Wadi Natroun was first cut off by desert from the Nile Valley and subsequently from the Nile Delta. Thus the patterns of geographic variation in the forms under consideration parallel the sequence of events that led to the complete separation of Wadi Natroun from the Nile Valley and Delta. However, it is possible that during the high water periods of the Holocene when the distance across the desert barrier would have been reduced *Prinia gracilis* dispersed from the Nile Delta to Wadi Natroun. The importance of vegetated zones between populations can be further supported by the fact that the Faiyum is a virtually disjunct oasis, but is still linked to the Nile Valley by a vegetated corridor, presumably through which genetic exchange takes place, accounting for the lack of differentiation between the populations of *P. gracilis* in the Faiyum and lower Nile Valley.

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Appendix 1.—Localities of *Prinia gracilis* material examined. *Cairo OTU*—Abu Rawash BMNH 2, FMNH 2, USNM 8; Cairo BMNH 2, ZFMK 2; Giza AMNH 3, BMNH 4, MCZ 2.

Wadi Natroun OTU—Wadi Natroun BMNH 8 (including holotype), FMNH 15.

Nile Delta OTU—Alexandria BMNH 2; Bahig DMNH 1; Bir Shams BMNH 1; Damietta BMNH 1; El Merg ZFMK 1; Idku, Rosetta FMNH 1.

Faiyum OTU—Faiyum BMNH 2; Kom Oshim FMNH 2; Lake Qarun (Moeris) BMNH 2; Tamiya AMNH 1.

Other Egyptian localities—Abu Simbil ZFMK 1; Amada DMNH 1; Armena YPM 10; Aswan USNM 1; "Balauyeh, Nubia" FMNH 1; Ismaliya USNM 2; Lake Menzala AMNH 1; "Luchess" or "Euchess" BMNH 1; Luxor AMNH 1, UMMZ 2; Port Said BMNH 7, FMNH 1, ZFMK 7, USNM 1; Qantara AMNH 1, BMNH 1; "Siout, E. of" FMNH 1; "Tartah" FMNH 2; Toshka YPM 2.

Sudan localities—Berber BMNH 1; Kaweimat ZFMK 1; Kerma AMNH 6; "Niakala" AMNH 1; Shendy AMNH 6, BMNH 1.